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CASTILLEJA AMBIGUA VAR. *MEADII* (OROBANCHACEAE): A NEW VARIETY FROM NAPA COUNTY, CALIFORNIA

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ABSTRACT

Castilleja ambigua var. ***meadii*** is described from Napa County, California. It is included within *Castilleja ambigua* based on the strong resemblance of the morphology, coloration, and markings of the corollas, as well as the coloration of the bracts. It is distinguished from the other named varieties of *C. ambigua* by its erect, typically unbranched stems and by its linear, often unlobed leaves and bracts with linear lobes. The new variety occurs in low relief, fresh water, vernally wet meadow associations on volcanically derived substrates. The new variety is an uncommon, very localized endemic whose conservation status is in need of prompt evaluation.

KEY WORDS: Orobanchaceae, Castillejinae, *Castilleja ambigua* var. *meadii*, new species, endangered species, chromosome numbers, Napa County, California

In 1986, Ruygt first encountered an unfamiliar annual *Castilleja* near Atlas Peak Road, northeast of the city of Napa, California, while conducting an inventory of native plants for a private landowner. The landowner previously recognized the unique character of the natural landscape in the Atlas Peak area and contacted Ruygt to find out more about the diverse selection of species on the property. A search of a small wetland complex on this property brought to light species not previously known to occur in Napa County, including the federally listed species *Navarretia leucocephala* Benth. subsp. *pauciflora* (H. Mason) Day, as well as the novelty described here. In 1987, Ruygt visited the original Atlas Peak site with L.R. Heckard (UC/JEPS). This site contains a seasonally wet meadow, a few small vernal pools, and upland grasslands. Heckard, an authority on the Castillejinae, tentatively identified the new form as *Orthocarpus lacerus* Benth., a species now known as *Castilleja lacera* (Benth.) Chuang & Heckard. Heckard deposited a voucher collection (*Heckard & Ruygt 6661*) at JEPS, which was apparently recently annotated as a genetic cross "between *C. attenuata* (A. Gray) Chuang & Heckard and *C. rubicundula* (Jeps.) Chuang & Heckard subsp. *lithospermoides* (Benth.) Chuang & Heckard, of hybrid parentage." No rationale was included with this annotation to justify the hybrid determination. Two additional populations of the new *Castilleja* were discovered in wetlands on the nearby Mead Ranch in 1990.

While working on a manuscript for a new flora for Napa County (in prep.), Ruygt decided to more closely compare the similarities of plant specimens of the putative disjunct populations of *Castilleja lacera* from Napa and Marin Counties with herbarium specimens from populations within the primary range of the species. This study revealed that the Marin County (*Esau s.n.*, UCD) and Napa County (*Esau s.n.*, JEPS, UCR) specimens were misidentified *Castilleja rubicundula* var. *lithospermoides* and that specimens of *C. lacera* from the main part of its range differed markedly in a number of characters from the Napa County novelty. This information prompted a field investigation, and in 2009 Ruygt visited a population of *Castilleja lacera* in McArthur-Burney Falls State Park, Shasta County, California. Photographs were taken along with a specimen collection (*Ruygt 5420a*, JEPS) for purposes of comparison in a "green" state of that species with the Napa County plants. This comparison convinced Ruygt that the Atlas Peak populations did not compare well morphologically with typical *C. lacera* and that they did not pertain to that species. In addition, the morphological uniformity of the Atlas Peak populations suggested that recent or current hybridization was not at play in this case.

After some futile attempts by Ruygt to obtain a satisfactory identification of the Atlas Peak populations based on studies at local herbaria, a photograph of a live plant taken by a participant on a California Native Plant Society wildflower hike on the Mead Ranch passed through e-mail channels, eventually connecting Ruygt with Egger in 2010. Egger recognized the unique features of the plants in question, and, after studying close-up digital images and a voucher collection (*Ruygt 5575*, JEPS, WTU) supplied by Ruygt, he also became convinced that the Atlas Peak populations represented an undescribed form of *Castilleja ambigua* Hook. & Arn. In May 2011, Egger and Ruygt visited two populations of *C. ambigua* var. *meadii*, including the type locality, confirming Egger's preliminary determination of the new variety, as described below.

CASTILLEJA AMBIGUA Hook. & Arn. var. **MEADII** J.M. Egger & J.A. Ruygt, var. nov. Figures 1, 3-7. **TYPE: USA. California.** Napa Co.: Mead Ranch, west of Atlas Peak Road, 2.4 km SW of Foss Valley, E 564639, N4250064, vernal pools in rocky meadow in shallow clay soil, with *Eryngium*, *Eleocharis*, on volcanic (Sonoma Formation) substrate surrounded by chamise-*Ceanothus*-oak chaparral, elevation 475 m, 28 May 2011, *J. Ruygt 5793* (holotype: WTU; isotypes: CAS, GH, MO, NY, US).

Similar to typical *Castilleja ambigua* Hook. & Arn. in the morphology, coloration, and markings of the corollas as well as the coloration of the bracts but differing from it in its erect, typically unbranched stems, its linear, often unlobed leaves, and its bracts with linear lobes. The new variety also differs in its preference for low relief, fresh water, and vernally wet meadow habitat on shallow, gravelly, volcanically derived substrates.

Plants annual, 6–22 cm tall, with thin, fibrous roots. **Stems** unbranched or less commonly with a few divaricate-ascending branches from the proximal half of the stem but above the base, purplish-brown, sparsely pilosulous with mix of shorter, stipitate-glandular hairs and longer, non-glandular hairs, both becoming longer, more often glandular, and more numerous distally, approaching the inflorescence. **Leaves** 1–5 cm long, linear, < 1 mm wide at the base, entire or with 1 (2) pairs of linear lobes, 2–8 mm long; pilosulous to hispidulous and often stipitate-glandular, especially abaxially. **Inflorescences** 1.5–6.0 cm long, with few to many, densely ranked, sessile to short-pedicillate flowers. **Bracts** 5–15 mm long, divided from near the base into 3–5 divaricate-ascending lobes, the central lobe linear to very narrowly linear-lanceolate, the lateral lobes linear; pilosulous to hispidulous and often stipulate-glandular; pale greenish proximally, often with a darker midvein, distal tips pale white, becoming greenish with age. **Calyces** 8–14 mm long, divided subequally into four linear lobes, each 5–9 mm long; pilosulous to hispidulous and stipitate-glandular, pale greenish proximally, often becoming pale yellowish distally. **Corollas** pale yellow, 14–21 mm

long, lower lip 3–4 mm wide, with three divergent, saccate pouches 2–2.5 mm wide, each with a dark reddish-purple spot near the tip at the base of the short, whitish, distal tooth, and often with a similar spot located near the base of each pouch; beaks 1–4 mm long, pale, densely puberulent. **Stigmas** exserted, ca. 2 mm wide, obscurely bilobed, stramineous when receptive, becoming darker with age. **Anthers** 0.8 mm long, exserted at full anthesis. **Capsules** 5–6 mm long, ovoid with a curved, acuminate tip, glabrous, stramineous. **Seeds** many, ca. 0.8 mm long, short-ovoid, brownish; coat tight-fitting, reticulate, cells mostly polygonal-ovate, radial walls moderately deep and horizontally striated, inner tangential walls membranous and apparently unruptured at maturity. **Chromosome number**: n = 12, based on counts made by Tank from the type gathering, *Ruygt 5793* (Fig. 8).

Four of the five known populations of *Castilleja ambigua* var. *meadii* occur on the Mead Ranch and are protected under a Conservation Easement with the Land Trust of Napa County. The Mead Family has set aside 1100 acres as "Forever Wild," and it is in recognition of the exemplary land conservation ethic of this family that the new variety is named.

Additional specimens examined. **USA. California**. Napa Co.: Population 1 (type locality): Giles Mead Ranch, 8.8 km E of Yountville, large meadow surrounded by Live Oak Woodland/ Chamise-*Ceanothus* Chaparral, 0.85 km WNW of main residence, 21 Apr 1990, *Ruygt 2489* (JEPS); Atlas Peak Road, S of Foss Valley, Yountville Quad. (7.5'), 6N 4W, S2, SE 1/4 of NE 1/4, 31 May 2010, *Ruygt 5575* (JEPS, WTU, tissue sampled for DNA sequencing by D. Tank, ID), 15 May 2011, *Egger 1468* (WTU). Population 2: Giles Mead Ranch, surrounded by Live Oak Woodland, ca. 0.3 km NW of main residence, live plants examined by Ruygt but population unvouchered and now apparently extirpated. Population 3: Giles Mead Ranch, surrounded by Live Oak Woodland, ca. 0.4 km W of main residence, live plants examined by Ruygt but unvouchered. Population 4: Giles Mead Ranch, surrounded by Black Oak Woodland, ca. 0.7 km NE of main residence, 28 May 2011, *Ruygt 5796* (JEPS). Population 5: 4.5 mi N of Westgate Dr. on Atlas Peak Rd., upper end of Milliken Canyon, 18 May 1986, *Ruygt 1777* (JEPS); 6.5 mi up Atlas Peak Rd. from Monticello Rd., 10 May 1987, *Heckard & Ruygt 6661* (JEPS).

Distribution and range

All populations of var. *meadii* occur within a highly localized district of the Atlas Peak plateau on a single site type characterized by very gradual slopes, shallow clay soils of volcanic origin, and numerous surface rock outcrops (rubble). Populations are known from 5 locations (Fig. 2), four that occur on the Mead Ranch, a 1300-acre property, largely under conservation easement with the Land Trust of Napa County (LTNC). One population on the Mead Ranch is now apparently extirpated, probably due to competitive pressure from invasive weed species including perennial grasses. The fifth population is partially protected by a conservation easement between a past landowner and the LTNC and now honored by the present owner. Additional populations may occur nearby on adjacent properties and in the Howell Mountain area to the northwest.

Phenology, ecology, and associated species

Castilleja ambigua var. *meadii* flowers from April through June in seasonally wet meadows, shallow vernal pools, and along the margins of ephemeral streams. The elevation of the known populations ranges between 450-475 m. The meadows in which this variety is found are typically small (< 10 acres) and surrounded by chamise-*Ceanothus* chaparral, mixed oak-foothill pine woodland, or black oak forest. It occurs in thin clay soils of the Aiken Series (Lambert & Kashiwagi, 1978), of volcanic origin. The bedrock is basic, of the Sonoma Volcanic Formation (< 5 million y.o.). Some sites are seasonally inundated and are classified as Northern Basalt Flow Vernal Pools, a Department of Fish and Game designated rare plant community (Holland 1986). Common associate species include *Eleocharis macrostachya* Britton, *Eryngium aristulatum* Jeps. var. *aristulatum*, *Holozonia filipes* (Hook. & Arn.) Greene, *Allium amplectans* Torr., *Downingia concolor* Greene, and

Isoetes spp. This is a diverse wetland community, including over 25 vascular plant species documented as near neighbors to *C. ambigua* var. *meadii*.

In at least one population (the type locality), *Castilleja attenuata* is a common associate of the new variety, often growing within centimeters of it. No evidence of any kind of hybridization or genetic introgression between these closely related annual *Castilleja* forms has been observed. The same is also true of *Castilleja densiflora* (Benth.) Chuang and Heckard, which occurs around the drier margins of some populations of *C. ambigua* var. *meadii*.

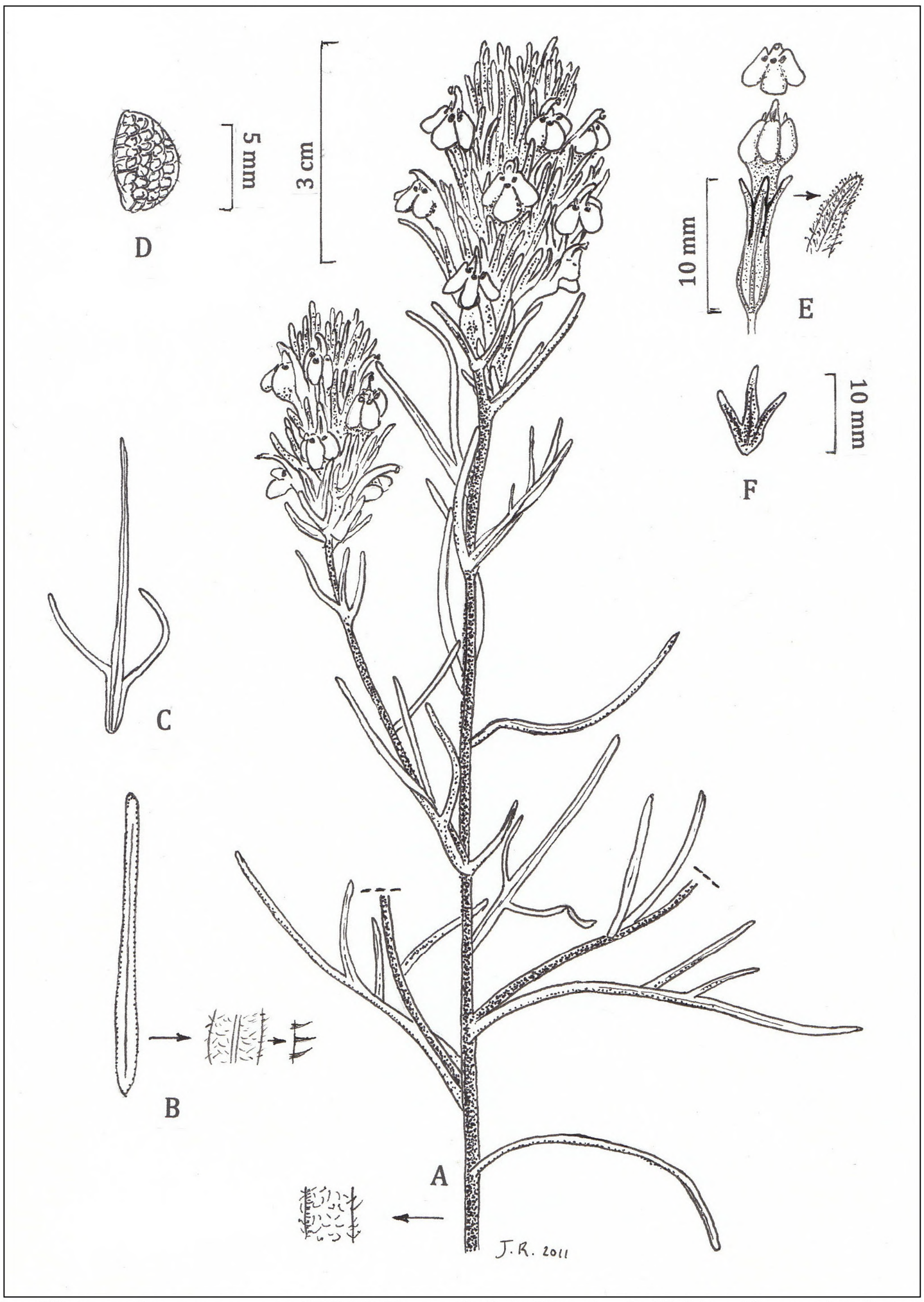

Figure 1. *Castilleja ambigua* var. *meadii* J.M. Egger & J.A. Ruygt. A. Habit with proximal stem pubescence detail and inflorescences. B. Proximal leaf with pubescence detail. C. Distal leaf. D. Seed coat. E. Calyx and corolla with calyx pubescence detail. F. Floral bract. Illustration by J. A. Ruygt.

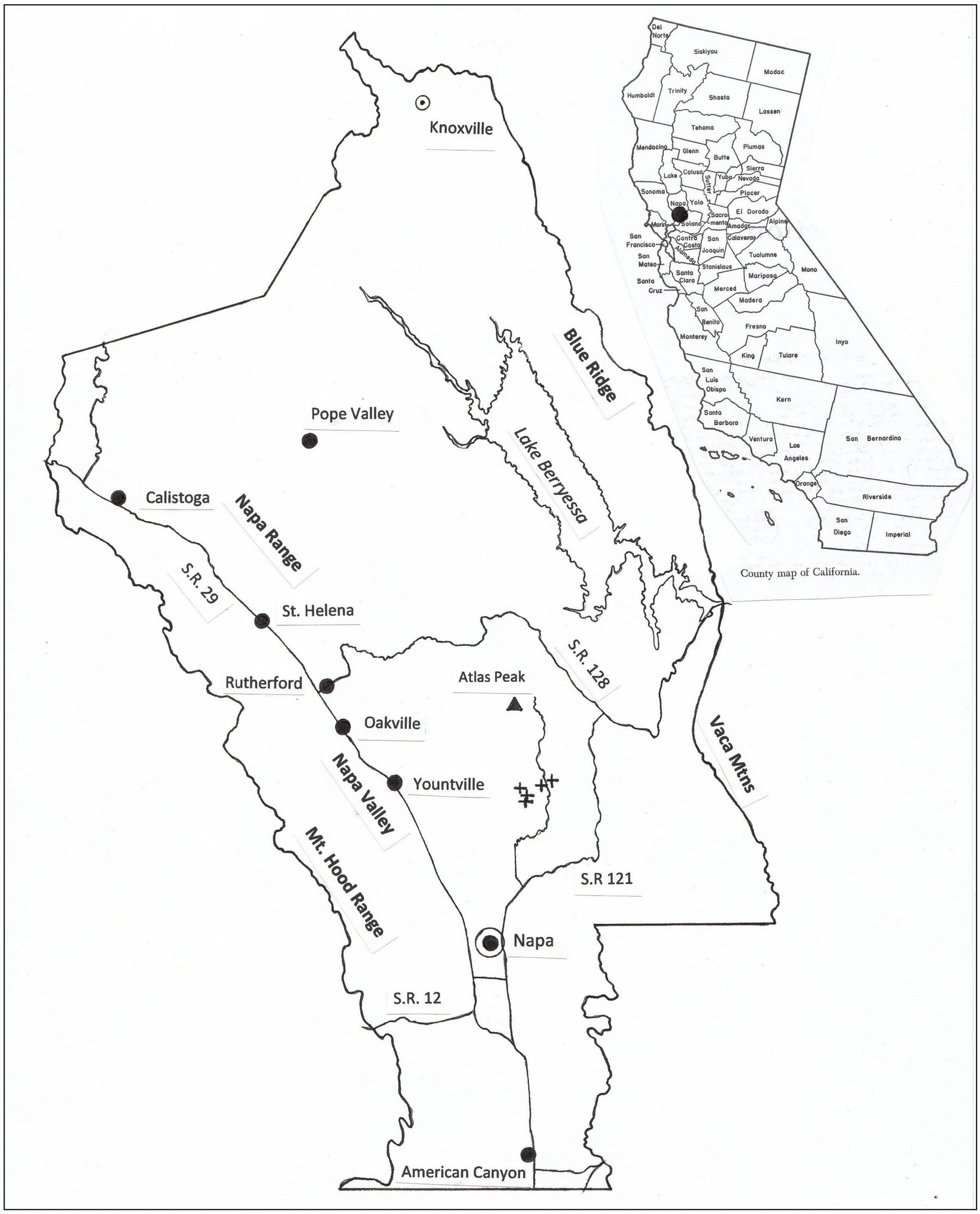

Figure 2. Range of *Castilleja ambigua* var. *meadii* within California and within Napa County. Populations of the new variety are indicated by + symbols on the Napa County map.

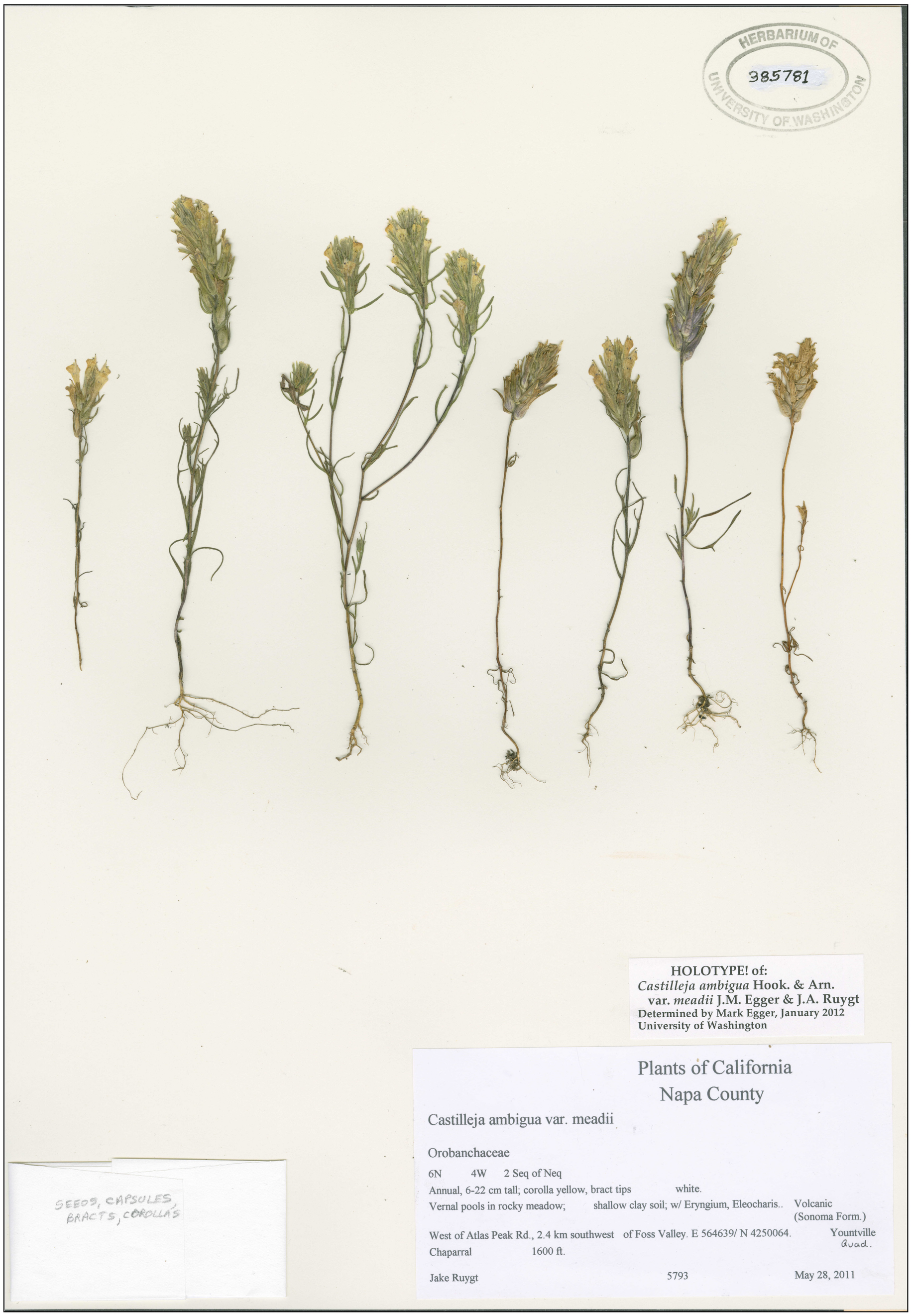

Figure 3. Holotype collection of *Castilleja ambigua* var. *meadii* (*Ruygt 5793*, WTU).

Figure 4. *Castilleja ambigua* var. *meadii*, cluster of plants in habitat. Photo by Mark Egger.

Figures 5-6. *Castilleja ambigua* var. *meadii*, inflorescence (L) and whole plant (R). Photos by Mark Egger.

Figure 7. *Castilleja ambigua* var. *meadii*, inflorescences and upper stem. Photo by Mark Egger.

Methods for chromosome counts. Immature floral buds were fixed in Carnoy's solution (3 part 100% EtOH: 1 part glacial acetic acid v/v; Chuang & Heckard 1993). Anther sacs were dissected from floral buds ca. 1.6–2.0 mm long and stained with aceto-carmine on a microscope slide. Microspore mother cells were released from the anthers, anther walls were removed, a glass coverslip was added, and the slide was then gently heated to just before boiling. To insure accuracy, chromosomes were counted from approximately 12 cells using 100x magnification on a Zeiss phase contrast microscope.

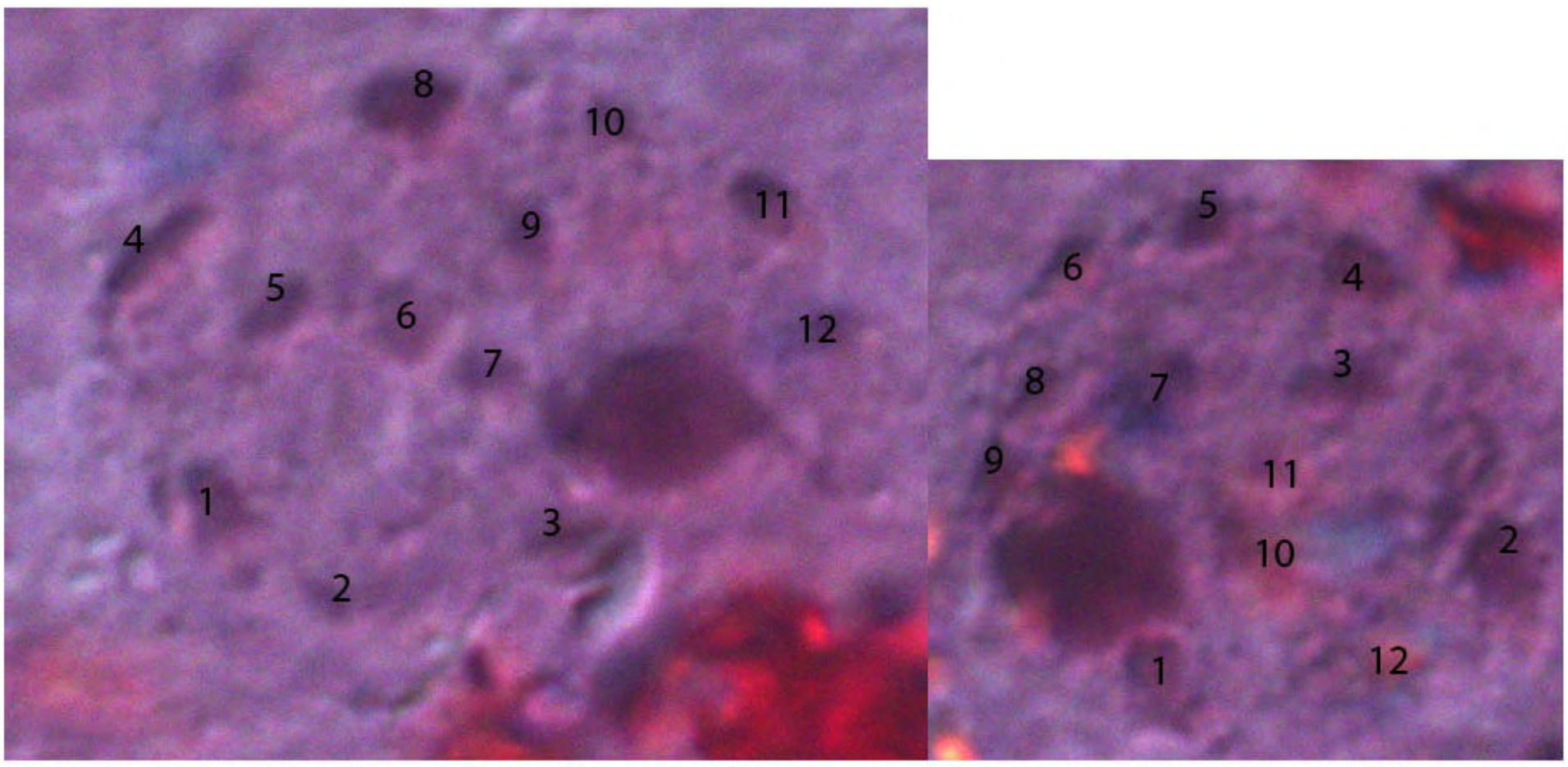

Figure 8. Photographs of two pollen mother cells of *Castilleja ambigua* var. *meadii* from *Ruygt 5793* showing numbered chromosome locations. Photos by David Tank.

Relationships and identification

Castilleja ambigua is a complex and polymorphic species endemic to the west coast region of North America, from southern California north to extreme southwestern British Columbia, Canada. It was previously placed in the formerly paraphyletic genus *Orthocarpus* Nutt. as *O. castillejoides* Benth. Jepson (1925) described *O. castillejoides* var. *insalutatus* Jeps., and Keck (1927, in his revision of *Orthocarpus*) added another infraspecific segregate, *O. castillejoides* var. *humboldtiensis* D.D. Keck. Later, *O. castillejoides* and the other species of the former *Orthocarpus* sect. *Castillejoides* A. Gray and sect. *Cordylanthoides* Keck were moved into *Castilleja* in Chuang and Heckard's revision of the Castillejinae (Chuang & Heckard 1991). At that time, Chuang and Heckard adopted the previously published name, *C. ambigua* Hook. & Arn. for *O. castillejoides* and changed the rank of the infraspecific groupings from variety to subspecies. Subsequently, Egger (2008) reestablished the use of varieties for the infraspecific categories within *C. ambigua*, as part of a broader attempt to provide a standardized nomenclature with the entire genus.

Castilleja ambigua var. *humboldtiensis* (D.D. Keck) J.M. Egger and *C. ambigua* var. *insalutata* (Jeps.) J.M. Egger are both strictly coastal, occurring in estuarine salt marshes and on sandy dunes and bluffs. The typical form of *C. ambigua* is more adaptable and far more widespread, occurring in a number of complex and variable forms both along the coast and somewhat sporadically in grasslands and meadow situations some miles in from the immediate coast.

We place the new variety within *Castilleja ambigua* due primarily to the morphology, coloration, and markings of the corollas, which are virtually identical to those found in many individuals of the nominate variety, as well as the whitish tips on the distal portion of the bracts. Indeed, the corollas of var. *meadii* could likely be exchanged with those of the typical variety without being noticed, even under magnification. Points of congruity include: pale yellow background coloration, a single reddish-purple marking at the base of each distal tooth of the each lobe of the lower lip of corollas, and, in many plants, a similar set of markings near the base of each inflated sac of the lower lip of the corolla. However, var. *meadii* is immediately and with ease separated from the other forms of *C. ambigua* by the characters noted in the key below, and the somewhat wispy plants are quite distinctive in the field (Fig. 9). It should also be noted that populations of the typical inland form of the nominate variety of *Castilleja ambigua* occur in the Foss Valley (*Ruygt 4432*), ca. 3 km

northwest of the nearest population of var. *meadii*, with no signs of intergradation between the two entities.

Phylogenetic research now underway at the University of Idaho will eventually clarify the relationships between *Castilleja ambigua* var. *meadii* and the other varieties of *C. ambigua*, as well as its placement within the genus as a whole.

Figure 9. The named varieties of *Castilleja ambigua* in the field. From left to right, var. *meadii*, var. *ambigua*, var. *humboldtiensis*, and var. *insalutata*. Photos by Mark Egger.

As noted above, an annotation of the collection *Heckard and Ruygt 6661* (JEPS) proposes that the new variety is of hybrid origin between *Castilleja attenuata* and *C. rubicundula var. lithospermoides*. While such a conjecture is not unreasonable based on a presumed intermediate morphology between these two species, there is little evidence to support this concept in the field. While this combination might reasonably apply to an F_1 hybrid between the two putative parent species, the populations of *C. ambigua* var. *meadii* are all quite uniform in morphology and show none of the wide variation of characters in typical hybrid swarms found regularly in *Castilleja* (Egger 1994 and unpubl. data). In fact, the plants both within and between the populations of var. *meadii* are more uniform in morphology than are those of many other widely accepted species within the genus.

Moreover, the meiotic chromosome number of n = 12 presented here is the base number for *Castilleja* (Chuang and Heckard 1991), indicating that the new variety is clearly not of allopolyploid hybrid origin. Both *C. ambigua* var. *ambigua* (Atsatt 1966; Chuang and Heckard 1982) and var. *humboldtiensis* (Anderson 1965) are also known only from counts of n = 12. While a homoploid hybrid origin for the new variety cannot be conclusively ruled out at this time, such a scenario seems unlikely, due to the lack of significant variation within and between the different populations. DNA analysis now underway by Tank should resolve the details of the relationships of var. *meadii* in the near future.

A simplified key for separating *Castilleja ambigua* var. *meadii* from other annual species of *Castilleja* occurring from the San Francisco Bay Region northward in California.

1. Bracts distally colored red to very occasionally yellow, lower lip of corollas rudimentary, greenish or reddish and not at all inflated ..... **C. minor**
1. Bracts distally colored rarely if ever as above, lower lip of corollas petaloid and slightly to strongly pouched.

2. Bracts colored uniformly greenish throughout ..... **C. lacera, C. rubicundula, C. tenuis**
2. Bracts proximally colored dully and more or less uniformly, but distally colored brightly and contrastingly, at least when emergent.

3. Bracts distally colored purplish to magenta or pink, rarely white and then mixed into populations of typically colored plants and greatly outnumbered by them .....**C. densiflora, C. exserta**
3. Bracts distally colored white to rarely pale yellowish.

4. Inflorescences slender, 10-20 mm wide; corollas more or less linear, the inconspicuous pouches about 2 mm wide; stigmas included within the corolla beaks .....**C. attenuata**
4. Inflorescences broadened, 20-40 mm wide; corollas widened distally, the conspicuous pouches usually 3-5 mm wide; mature stigmas usually exserted from the corolla beaks.

5. Leaves and bracts entire and more or less lanceolate ..... **C. campestris**
5. Leaves usually divided or less commonly a mixture of divided and undivided leaves, bracts always divided and not as above.

6. Plants stems more or less decumbent, at least proximally, usually branched, often profusely; lobes of leaves and bracts lanceolate to broadly lanceolate and often distally rounded; plants of various habitats, including coastal salt marshes, the margins of brackish estuaries, coastal sandy bluffs, and mesic to somewhat xeric inland grasslands .....**C. ambigua**, incl. var. **humboldtiensis** and var. **insalutata**
6. Plants stems upright, usually unbranced, uncommonly with a few ascending branches, lobes of leaves and bracts linear; plants of gravelly, vernally moist, inland meadows in volcanically derived soils ..... **C. ambigua** var. **meadii**

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